Response of Broom Snakeweed (*Gutierrezia sarothrae*) and Cool-Season Grasses to Defoliation

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Broom snakeweed is one of the most widespread range weeds in western North America. Although a native plant, it increases with disturbance such as overgrazing, fire, and drought, and can dominate sites. The objective of this study was to test the hypothesis that defoliation of broom snakeweed alone, and along with associated grasses, would reduce its vigor and increase its mortality in bunchgrass plant communities. The study was conducted at two locations: near Nephi, UT in an invaded crested wheatgrass stand and at Howell, UT in a bluebunch wheatgrass/Wyoming big sagebrush community. Clipping treatments consisted of (1) untreated Control; (2) All Clip—clipping all herbaceous vegetation 2 cm above the soil surface, and current season foliar growth of snakeweed; (3) Grass Clip—clipping all grass and forb plants; (4) Snakeweed Clip—clipping current season foliar growth. Treatments were randomly assigned to 1-m^2 plots and clipped in May or late August. Plots were measured and clipped at the respective seasons annually from 2004 to 2007. Defoliation of snakeweed in spring in the Snakeweed Clip treatment caused higher mortality and lower size and vigor of remaining plants than the other treatments at the end of the study. Clipping all vegetation also reduced snakeweed density at Nephi, but not at Howell. There was little regrowth of bluebunch wheatgrass at Howell in the All Clip treatment; thus, it was likely to have not competed with snakeweed regrowth for limited soil moisture. Bluebunch wheatgrass cover declined at Howell in the All and Grass Clip treatments. Crested wheatgrass was not adversely affected by spring defoliation in the All and Grass Clip treatments, and it increased in the Snakeweed Clip treatment. There were few differences in the fall defoliations. Spring defoliation of snakeweed put it at a competitive disadvantage with both intact perennial bunchgrasses and regrowth crested wheatgrass, thus enhancing its mortality.

Nomenclature: Broom snakeweed, *Guterrezia sarothrae* (Pursh) Britt. & Rusby GUESA; bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) A. Love; crested wheatgrass, *Agropyron cristatum* (L.) Gaertn.; Wyoming big sagebrush, *Artemisia tridentata* var. *wyomingensis* (Beetle & A. Young) Welsh.

Key words: Biological control, cattle grazing, plant defense strategy, poisonous plant.

Broom [*Guterrezia sarothrae* (Pursh) Britt. & Rusby] snakeweed is one of the most undesirable plants on western rangelands (Platt 1959). Although a native plant, it increases with disturbance such as overgrazing (McDaniel and Torrell 1987), fire and drought (USFS 1937), and dominates sites in the creosote bush, desert grassland, short-grass prairie, salt-desert shrub, sagebrush steppe, and pinyon/juniper plant communities. It is easily controlled with herbicides (McDaniel and Duncan 1987) and fire (McDaniel et al. 1997), but its seed bank in soil enables it to come back in wet years. It is toxic to livestock, causing abortions (Dollahite and Anthony 1957). However, Ralphs et al. (2007) forced cattle to graze it for up to 20% of their diets without any adverse effects, and suggested livestock grazing might be a practical control of snakeweed.

The goal of using livestock grazing as a control of weeds is to manipulate the patterns of defoliation to place the target plant at a competitive disadvantage relative to other plants in the community (Vallentine 1989). Plant defense theories (Bryant et al. 1983; Cooley et al. 1985; Feeny 1976; Herms and Mattson 1992; McKey 1974; Rhoades and Cates 1976) suggest plants accumulate high levels of secondary defense compounds at the expense of growth. If highly defended plants are subsequently defoliated, they are at a substantial disadvantage compared to fast-growing species that are grazing-tolerant, such as grasses (Briske and Richards 1995). Broom snakeweed contains terpenes and

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Interpretive Summary

Broom snakeweed is one of the most widespread range weeds in western North America. It increases and dominates plant communities following overgrazing and fire. Although overgrazing is a principal cause of its increase, targeted grazing might be an effective biological control. A defoliation study was conducted to determine if clipping snakeweed by itself, and along with associated grasses, would decrease its vigor and cause mortality. Following clipping of all vegetation simulating heavy grazing, crested wheatgrass recovered from defoliation and provided competition that caused a greater mortality of mature snakeweed plants. Bluebunch wheatgrass did not recover from defoliation and did not provide competition to increase snakeweed mortality. This supports the strategy of targeted grazing to force cattle to graze snakeweed that has invaded crested wheatgrass stands, as a biological control tool.

total resins ranging from 6 to 13% of the dry weight of the plant (Ralphs et al. 2007); thus, it would be classified as having high level of carbon-based chemical defenses.

The objective of this study was to test the hypothesis that defoliation of broom snakeweed alone, and in combination with associated grasses, would reduce its vigor and increase its mortality in bunchgrass plant communities. I hypothesized that defoliation of snakeweed, leaving grasses intact, would cause the greatest mortality and loss of snakeweed vigor. Defoliation of both snakeweed and grasses still would be detrimental to snakeweed because the grasses should recover rapidly and utilize soil moisture and nutrient resources. Defoliation of grasses, leaving snakeweed intact, would accelerate the growth and dominance of snakeweed.

Methods and Materials

The study was repeated in two plant communities. The first site was 6 km [3.8 mi] southeast of Howell, UT (41°43′35.645″N, 112°23′8.491″W, elev. 1,554 m [5,100 ft]) within the Wyoming big sagebrush [*Artemisia tridentata* var. *wyomingensis* (Beetle & A. Young) Welsh.]/ bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Love] plant community. The aspect was a north-facing slope, and soils were loamy skeletal frigid calcic Argixerols. Wyoming big sagebrush was sparse (10% canopy cover); bluebunch wheatgrass was the dominant grass, with Sandberg bluegrass (*Poa secunda* J. Presl) being abundant, and forbs included *Phlox* spp., *Lupinus* spp., and western yarrow (*Achillea millefolium* L.). Broom snakeweed was uniformly scattered throughout the site.

The second site was 12 km west of Nephi, UT (39°43′44/702″N, 111°53′28.891″W, elev. 1,542 m). The original plant community was a Wyoming big sagebrush/Indian ricegrass [*Oryzopsis hymenoides* (Roem. & Schult.) Rickerox Piper] community, but a wildfire burned the site in July 1998 and it was seeded the following winter to

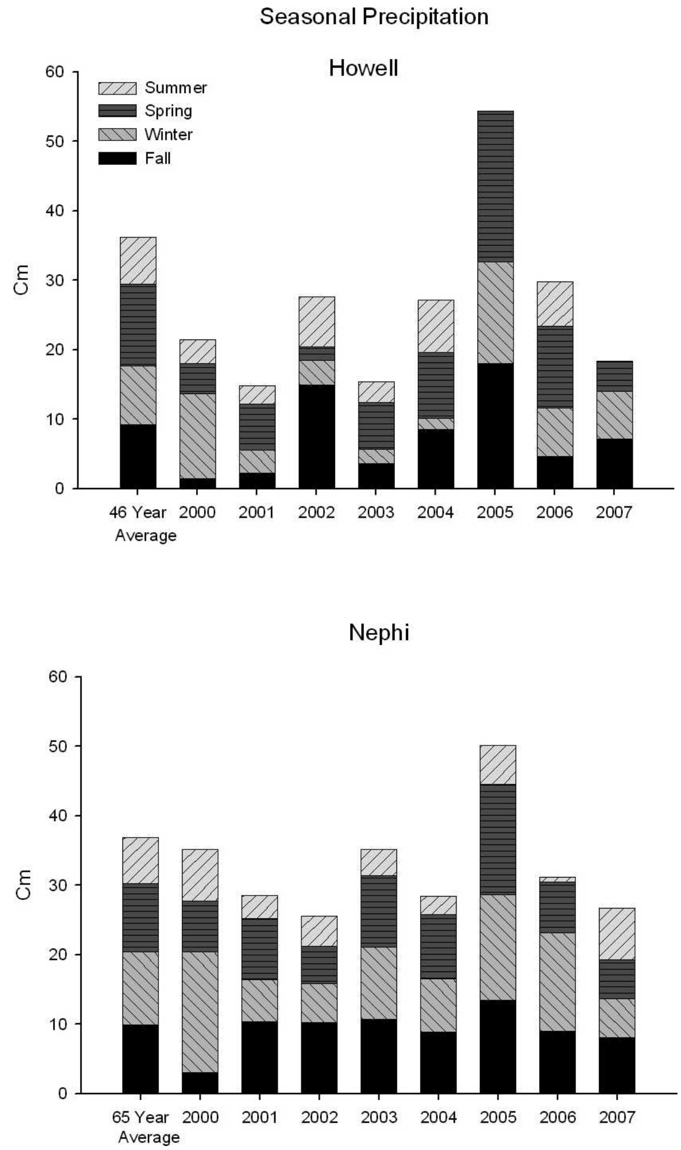

Figure 1. Seasonal water year precipitation during the study and long-term average at Howell and Nephi, UT.

crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.]. Remnant plants of Indian ricegrass remained, along with Sandberg bluegrass, downy brome (*Bromus tectorum* L.), *Phlox* spp., and browse milkvetch (*Astragalus cibarias* Sheldon). Snakeweed had reinvaded the site and was dense. Seasonal precipitation was obtained from the Nephi airport (about 5 km east of the Nephi site at about the same elevation), and from the Thiokol weather station 8 km south east of the Howell site (Figure 1).

Broom snakeweed is a suffrutescent half-shrub, meaning new stems arise from a woody crown each spring and die back in the fall. Therefore, the defoliation treatment removed only current season growth. Clipping treatments consisted of: (1) untreated Control; (2) All Clip—all herbaceous vegetation (grass and forbs) was clipped 2 cm above the soil surface, and current season foliar growth of snakeweed was clipped, leaving the crown intact; (3) Grass Clip—clipping all grass and forbs (forbs were a minor component of the plant community), leaving snakeweed plants intact; and (4) Snakeweed Clip—clipping current season foliar growth from mature and juvenile snakeweed plants. A new crop of snakeweed seedlings germinated and established in the wet year 2005. Seedlings were not clipped, but surviving juvenile plants were clipped in 2006 and 2007.

Clip treatments were randomly assigned to one of four, 1-m^2 plots laid out in a cluster. The plots were permanently marked with fiberglass pegs. Ten clusters of treatment plots were clipped in May (Spring) before culm elongation of grasses and during rapid growth of snakeweed, and another set of 10 clusters were clipped in late August (Fall) while grasses were dormant and snakeweed was in flower. The treatment vegetation was clipped 50 cm (2 in) beyond the plot boundaries to prevent any edge effect. Plots were considered the experimental unit to which treatments were randomly applied, and the clusters were considered blocks.

Prior to clipping each year, the following vegetative measurements were taken. The number of snakeweed plants was counted and classified as mature, juvenile ($<$ 7 stems), and seedlings (single stem). The height of each snakeweed plant was measured, and foliar diameter was measured from two perpendicular directions, from which conical canopy volume was calculated. Foliar cover of individual species was measured by the line intercept method along a 1-m tape stretched over the plot at three, 33-cm intervals. Plots were measured and clipped at the respective seasons annually from 2004 to 2007. Density of snakeweed age classes was counted for a final time in 2008.

A crude resin fraction was extracted from snakeweed samples in 2007. Five juvenile and five mature plants were collected on a monthly basis, dried in a forced air drying oven at 60 C (140 F) for 48 h and ground. A 0.5 g subsample was extracted with 10 mL methylene chloride for one hour, and then filtered into an Erlenmeyer flask. The solvent was removed by evaporation on a heating plate, and the extract was washed into tarred 8-mL vials. The solvent was completely removed by placing the vials on a heating block with nitrogen flow, followed by a vacuum for 15 min. The vials were weighed and the crude resins were calculated as a percentage of dry matter.

Snakeweed density, height, and volume, and species cover were analyzed in a repeated measures mixed model analysis of variance, comparing fixed effects of locations, seasons and clipping treatments. The random effect was clusters within locations and season, and years were the repeated measures. Where significant treatment-by-year interactions occurred, the model was reduced and the fixed effects were compared at the end of the study using the initial 2004 values as covariates.

Results and Discussion

Mature Snakeweed Plants. Initial density (2004) of broom snakeweed at Howell was 8.2 plants/m^2, and 4.5 plants/m^2 at Nephi. There was a natural reduction in the snakeweed population at both locations, in response to the continuing region-wide drought (Figure 1). There was a location-by-season interaction in density of mature snakeweed plants ($P = 0.01$), so the data are presented for locations and seasons separately. Following 3 yr of defoliation, density of mature plants was lowest in the spring Snakeweed Clip treatment at both locations ($P < 0.007$, Figure 2). At Nephi, mature snakeweed density in the spring All Clip treatment was similar to that of the Snakeweed Clip treatment. The stress of clipping, along with competition from grasses in the Snakeweed Clip treatment at both locations, and regrowth of crested wheatgrass in the All Clip treatment at Nephi, combined to reduce the density of the original mature snakeweed plants beyond the natural die-off during the drought.

In fall at Nephi, Snakeweed and All Clip treatments reduced mature plant density in 2005 ($P = 0.004$). The Control and Grass Clip treatments suffered a natural decline over the next 2 yr, so the final snakeweed density was between 1 and 2 plants/m^2 in all treatments. There were no differences among treatments in the fall at Howell.

Height and volume of snakeweed plants declined over the study (Table 1). Most of the larger (and presumably older) snakeweed plants died out in all treatments. There were no differences between locations in snakeweed height or volume ($P > 0.11$; thus, the data were pooled across locations. At the end of the study, height of snakeweed plants in the Snakeweed Clip treatment was 6.3 cm, compared to 11.5 cm in the All Clip treatment, and an average of 14 cm in the Grass Clip and Control treatments ($P = 0.0001$, Table 1). There was a seasonal effect of clipping on snakeweed volume ($P < 0.0001$). Foliar volume was about 50% greater in fall, reflecting the continued seasonal growth. Volume of snakeweed plants clipped in spring was only 15% of the control plants, compared to 36% of the control plants in the fall ($P < 0.05$, Table 1).

There was a season-by-treatment interaction in snakeweed cover ($P < 0.0001$). In the spring Snakeweed Clip treatment, cover of snakeweed declined and remained low throughout the study (Figure 3). In contrast, the Grass Clip treatment had the greatest snakeweed cover. Snakeweed cover in the All Clip treatment increased in 2007, in response to the large number of seedlings that established in the All Clip treatment in 2005, and continued to grow in size in 2006 and 2007 (see below). With fall clipping, snakeweed cover followed the density trends, with its cover declining in the Snakeweed Clip and All Clip treatments in 2005, then leveling out to where there were no differences among treatments at the end of the study.

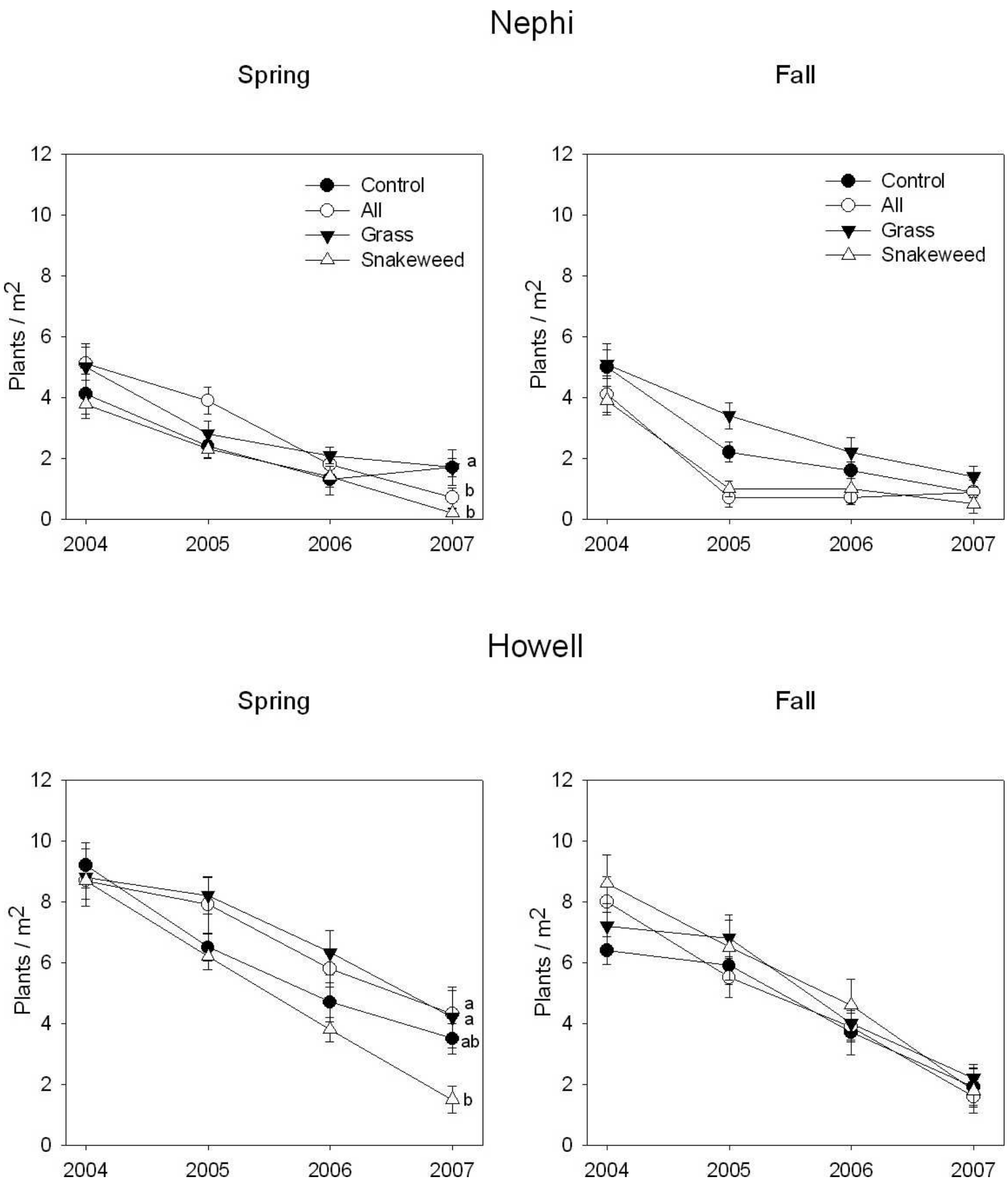

Figure 2. Density of mature snakeweed plants over time in response to clipping treatments at Nephi and Howell, UT.

Table 1. Height and volume of remaining mature snakeweed plants in 2007, compared to the initial values in 2004.

		Volume[a]	
Clip treatment	Height[a]	Spring	Fall
	cm	cm^3	
Control	13.7a	2,338a	3,425a
Grass Clip	14.3a	2,863a	2,911ab
All Clip	11.5ab	1,695ab	3,015ab
Snakeweed Clip	6.3b	336b	1,219b
Initial value	24	4,884	13,009

[a] Means within columns followed by different letters differ ($P < 0.05$).

There was a location-by-season-by-treatment interaction in bunchgrass cover ($P = 0.03$). Clipping bluebunch wheatgrass at Howell in the spring in both the Grass Clip and All Clip treatments reduced its cover (Figure 3). In contrast, its cover doubled in the Snakeweed Clip and Control treatments. Clipping affected bluebunch cover to a lesser degree in the fall. Clipping of crested wheatgrass at Nephi in the spring in the Grass Clip and All Clip treatments did not reduce its cover. However, its cover increased in the other two treatments. There were no differences among treatments or over years with fall clipping.

Grass morphology is such that the apical meristem is not elevated until elongation of the flower stalk. Defoliation of leaves prior to stem elongation allows intercalary meristems

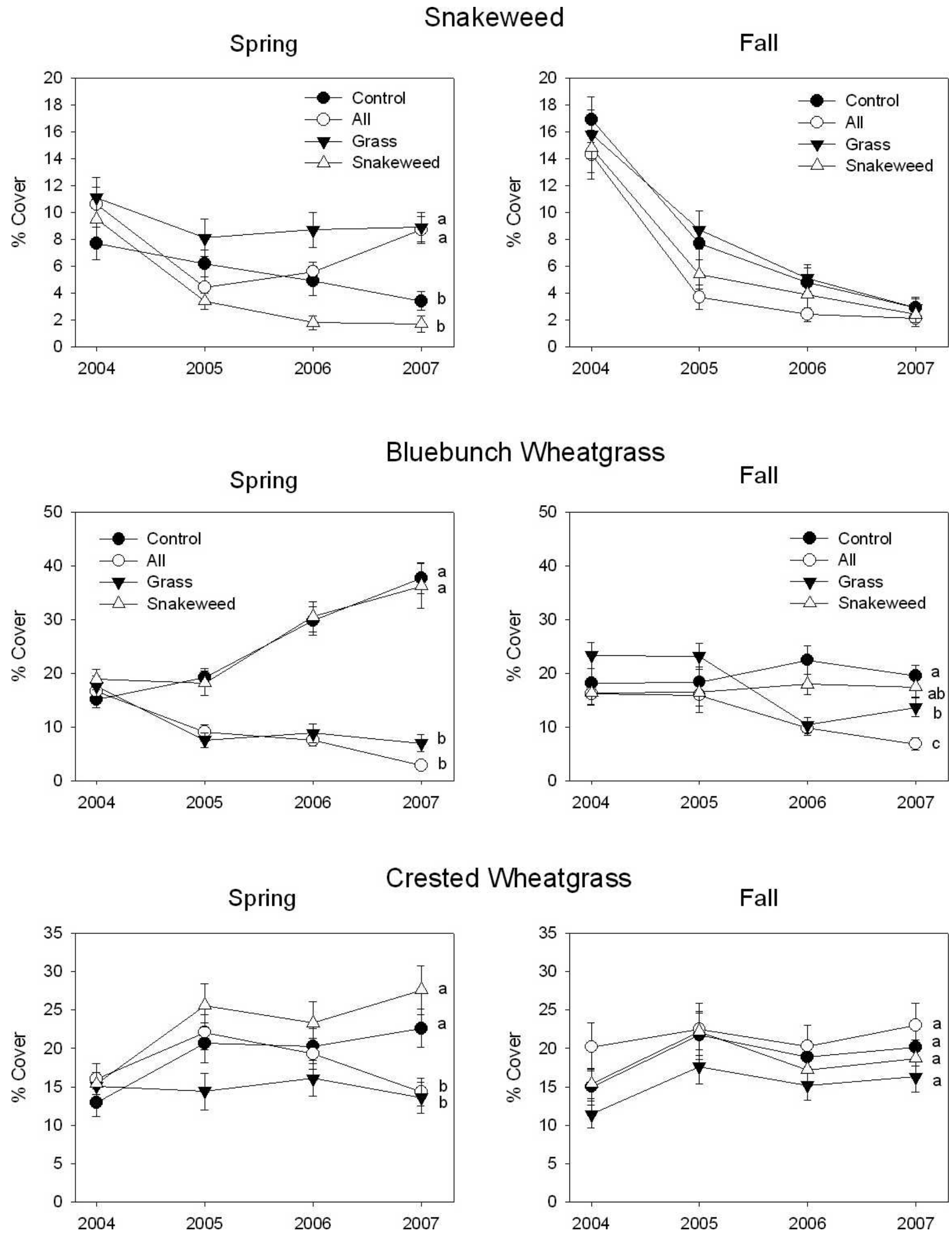

Figure 3. Foliar cover of snakeweed at both locations in Utah, bluebunch wheatgrass at Howell, and crested wheatgrass at Nephi, UT, in response to clipping treatments.

at leaf bases to continue to differentiate and elongate (Briske and Richards 1995; Dahl 1995), and rapidly replace photosynthetic leaf tissue to support continued growth of the plant. In contrast, the apical meristem of snakeweed is located at the tip of the stem. Any level of defoliation would remove this in both spring and late summer grazing trials, and any further growth must come from the slow process of new bud development from the crown.

The ability of a plant to respond to defoliation is not only determined by an inherent suite of morphological and physiological characteristics, but also by competitive pressure from associated species (Caldwell 1984; Mueggler 1972). The interaction between defoliation and competition is apparent in our study. Treatments in which we clipped only snakeweed and left grasses intact caused greater snakeweed mortality, and size of plants declined more than in the treatment in which we clipped grasses and

Table 2. Density of a new crop of snakeweed plants that germinated in the wet year 2005 and subsequently progressed to seedlings, juveniles, and mature plants (progression in bold). Data are presented for treatments clipped in spring.[a]

		Howell[b]			Nephi[b]		
Age	Clip treatment	2006	2007	2008	2006	2007	2008
		plants/m^2					
Seedling	Control	**1.5c**	1.6a	0.1a	**16b**	6a	2.6a
	All	**6.2ab**	2.7a	0.1a	**57a**	13a	0.7a
	Grass	**7.9a**	3.1a	0.1a	**42ab**	14a	1.6a
	Snake	**2.9bc**	1.0a	0a	**21b**	8a	0.5a
	Mean[c]						
	Fall clip mean	1.0	0	0.1	4.7	1.1	2.0
Juvenile	Control	1.6b	**0.9b**	0.1a	2.5b	**15c**	1a
	All	8.3a	**8.3a**	0.3a	20.5a	**60a**	3.7a
	Grass	3.0b	**10.5a**	0.8a	8.4b	**35b**	4.6a
	Snake	1.6b	**1.6b**	0.2a	4.6b	**13c**	1.9a
	Mean[c]						
	Fall clip mean	1.7	1.3	0.1	9.4	13	0.9
Mature	Control	—[b]	—[b]	**1.9bc**	—	—	**15bc**
	All	—	—	**5.2ab**	—	—	**22ab**
	Grass	—	—	**8.7a**	—	—	**32a**
	Snake	—	—	**0.5c**	—	—	**6c**
	Mean[c]						
	Fall clip mean	—	—	2.6	—	—	9.2

[a] Seedlings germinated in 2005 following above-average precipitation. Seedlings and juveniles in 2006 and 2007 progressed to mature plants in 2008 as denoted by bold type.

[b] Means within columns and age groups followed by different letters differ ($P < 0.05$).

[c] There were no differences between treatment in the fall, thus the fall clip mean at treatments is presented.

left snakeweed intact. The undefoliated grasses utilized the limited soil moisture and nutrients, thus limiting recovery of the snakeweed plants, which increased their mortality and reduced the size of remaining plants.

Clipping all vegetation had mixed responses at the two locations. Mortality of mature snakeweed plants was similar between the Snakeweed Clip and All Clip treatments at Nephi. Apparently, crested wheatgrass at Nephi was able to recover from the clip treatments and utilize the remaining soil moisture, thus exerting more competition on the defoliated snakeweed plants. Bluebunch wheatgrass at Howell apparently did not recover from defoliation in the All Clip treatment. Its cover continued to decline similar to the Grass Clip treatment. Therefore, lack of grass competition in the All Clip treatment at Howell allowed clipped snakeweed plants to survive.

Bluebunch wheatgrass at Howell was more sensitive to spring defoliation than was crested wheatgrass at Nephi. Even though grasses were defoliated at the least sensitive time prior to culm elongation (Caldwell et al. 1981), bluebunch wheatgrass cover declined by 50% under the clip treatments, whereas the cover of unclipped plants doubled.

Defoliation was not detrimental to crested wheatgrass, nor was competition from intact snakeweed plants. Crested wheatgrass is able to rapidly replace photosynthetically active leaf tissue (Caldwell et al. 1981; Olson and Richards 1988; Richards and Caldwell 1985), and extract water from soil at a higher rate because of its greater total root length and root growth in winter and early spring (Eissenstat and Caldwell 1988) than bluebunch wheatgrass. Removal of snakeweed competition allowed crested wheatgrass to increase over the study. Total removal of snakeweed plants in pinyon/juniper woodlands in New Mexico (McDaniel et al. 1982) and mesquite savannahs in Texas (Ueckert 1979) allowed blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths] to increase production 833% and 324% respectively. However, partial thinning of snakeweed plants did not result in increased grass production. The remaining plants simply increased in size and continued to dominate the plant community.

New Seedlings. A new crop of snakeweed seedlings germinated in 2005 in response to above-average spring precipitation. There were more seedlings and subsequently

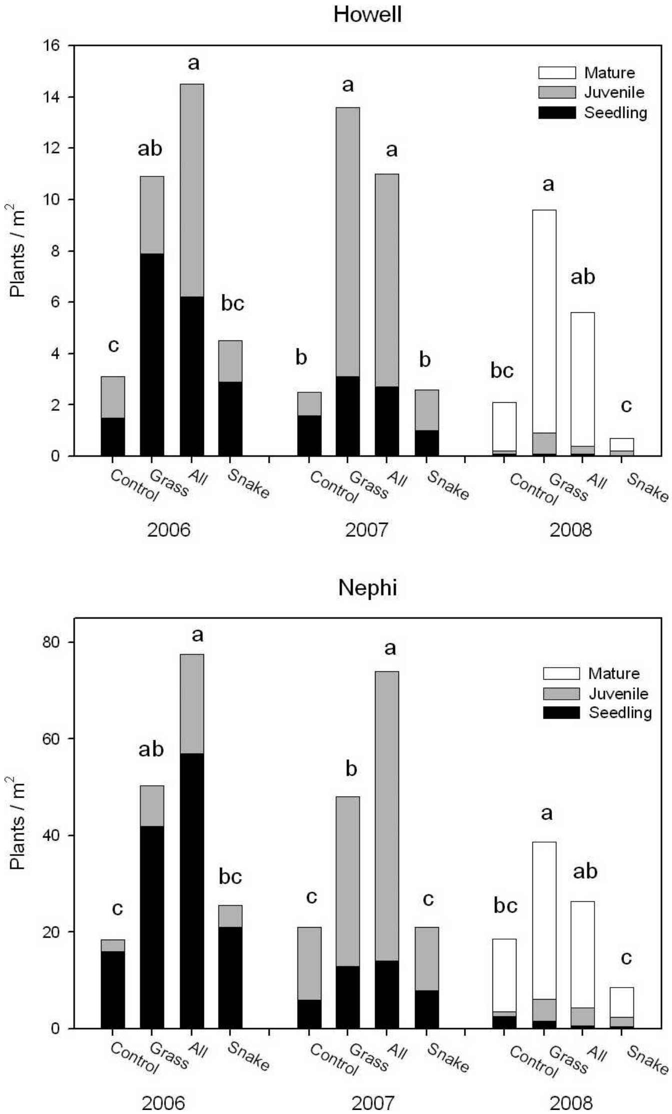

Figure 4. Germination of a new crop of snakeweed seedlings in the spring clipping treatments, following above-average spring precipitation in 2005. Snakeweed seedlings and juveniles in 2006 and 2007, progressed to mature plants in 2008. Within years, treatments having different letters differ ($P < 0.05$).

juveniles at Nephi than at Howell (Table 2). In spring 2006, density of seedlings at both Howell and Nephi was higher in the All Clip and Grass Clip treatment (Figure 4). These two treatments reduced the immediate demand for soil moisture, thus allowing new seedlings to establish and grow during the spring when soil moisture was available. There was no difference in seedling density among clipping treatments in fall.

There was a season by year by treatment interaction for juveniles ($P < 0.02$). The All Clip and Grass Clip treatments allowed the large number of seedlings in 2005 to survive and grow into vigorous juveniles in 2006 and 2007 (Table 2; Figure 4). At Nephi, the All Clip treatment had the greatest number of juveniles. Even though the juveniles were clipped in the All Clip treatment in 2006 and 2007, they survived and flourished in 2007 as a result of the reduced competition from grasses. However in 2008, the number plants progressing to mature snakeweed plants declined to a greater degree in the All Clip treatment, whereas the number of mature plants in the Grass Clip and Control treatments remained the same as the juveniles in 2007 (Figure 4). Perhaps the intraspecific competition among the large number of snakeweed plants in the All Clip treatment caused the dieoff.

The new fluctuating resource availability theory of invisibility (Davis et al. 2000) suggests that a plant community becomes more susceptible to invasion whenever there are unused resources. This occurs when there is either an increase in resource supply (high water year of 2005), or a decrease in resource use following disturbance (such as defoliation which reduced immediate water use by the dominant grasses). Reduction in grass demand for soil moisture in spring in both the All Clip and Grass Clip treatments allowed the snakeweed seedlings to survive into 2006, and they grew into vigorous juveniles in 2007, in spite of being clipped. At Nephi, juveniles had the greatest density in the All Clip treatment. Apparently, defoliation of all vegetation reduced competition from grasses and mature snakeweed, leaving sufficient soil moisture for juveniles to recover and survive. This contradicts the weed control theory that weeds might be more sensitive to defoliation than grasses that evolved with grazing (Briske and Richards 1995). However, intraspecific competition among mature snakeweed plants in the All Clip treatment might have caused their die off in 2008.

Crude resin content of juveniles was about half that of mature snakeweed plants in 2007 (10% vs. 17% crude resin at its peak during flowering, dry matter basis). This apparently contradicts the Optimal Defense Theory that states young immature tissue should have the highest concentration of secondary defense compounds (McKey 1974). However, the Growth/Differentiation Balance Theory (Herms and Mattson 1992) states there is a tradeoff between growth and defense. During rapid new growth, plants invest higher proportions of resources into cell division, elongation, and development of structures associated with growth, to further enhance resource acquisition, than to defense compounds. Perhaps young snakeweed plants put more resources into growth than chemical defense, allowing them to become well established and survive defoliation. In a study of palatability of redberry juniper trees, monoterpene concentration in new sprouts was an order of magnitude lower than in mature trees (Taylor et al. 1997).

Outbreaks of snakeweed populations can be triggered in years of above-average precipitation when there is excess soil moisture to allow seedlings to establish (McDaniel 1989; McDaniel and Ross 2002; Ralphs and Banks 2008; Ralphs and Sanders 2002; Thacker et al. 2008). Our study showed that even in healthy stands of native bluebunch wheatgrass or seeded crested wheatgrass, defoliation of these bunchgrasses in spring and subsequent reduction in their demand for soil moisture, might allow snakeweed seedlings to establish. However, the study also showed that defoliation of mature snakeweed plants, in combination with competition from regrowth of crested wheatgrass, can increase snakeweed mortality and reduce its size and vigor.

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